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PREDICTABLE SEQUENCES OF SPECIES LOSS WITH DECREASING ISLAND AREA - LAND BIRDS IN TWO ARCHIPELAGOES

Summary: We quantify the notion of predictable species loss from progressively smaller islands, and apply the quantification to the indigenous forest-dwelling birds of a series of New Zealand islands and to the passerines of the Cyclades Archipelago in the Aegean Sea. The analysis focuses on the reasons why the species-area relationship deviates from a perfect rank-correlation. For both avifaunas, most species are found remarkably predictably: they approximate a pattern in which each species occupies all those and only those islands larger than some species-specific minimum area. However, a minority of species in each avifauna do not conform to this pattern. Possible reasons for non-conformance include habitat differences among islands, anthropogenous extinctions, and equilibrium turnover. To the extent that the first two forces predominate, it would be far better to base conservation decisions on species lists from particular tracts that are potential refuges than on island occupancy patterns.

Keywords: Island biogeography; island avifauna; forest patches; reserves; conservation; species loss; New Zealand; Cyclades.

Introduction

It is a commonplace that larger sites, all other things being equal, tend to contain more species than do smaller ones. This "species-area" relationship dates back to at least 1835 (Connor and McCoy, 1979) and is viewed by Schoener (1976) as "one of community ecology's few genuine laws," but its basis is poorly understood (Connor and McCoy, 1979; McGuinness, 1984). At least four explanations have been proposed (McGuinness, 1984):

a) *The random placement hypothesis:* If species colonize sites analogously to raindrops falling into buckets, larger sites would have more species.

b) *The habitat diversity hypothesis:* Larger sites have more habitats, and each habitat has its own complement of species.

c) *The equilibrium theory hypothesis:* Species immigrate and go extinct at any site. Smaller sites have smaller populations, so extinction rates are higher, and more species are thus locally extinct at any particular time at small sites.

d) *The disturbance hypothesis:* Small sites suffer greater disturbance, and disturbance removes species or makes sites less suitable for species.

The hypotheses are not mutually exclusive, but even if all forces were operating, one would still like to know which is most important. The shape of the species-area curve cannot weigh in favor of one of these hypotheses over the others (McGuinness, 1984), and there is little direct study of the causes of the sepcies-area relationship for most archipelagoes of sites. In particular, there is very little evidence that turnover rates are higher on smaller islands than on large ones (Simberloff, 1976; Rey, 1981), as demanded by the equilibrium theory hypothesis. The oldest hypothesis, that of habitat diversity, derives much support from the careful autecological study of habitat requirements of particular species, while several studies of small marine habitats demonstrate the effect posited by the disturbance hypothesis (McGuinness, 1984).

Conservation implications of the species-area relationship are murky. Wilson and Willis (1975) argued that future species loss from reserves can be estimated from species-area curves of island biotae, and that the typical doubling of species richness for ten-fold area increase mandates the preservation of the largest possible sites. It is difficult to conceive of anyone favouring, *ceteris paribus,* a smaller site for a refuge over a larger one. But all things are never equal. Habitat is never completely identical between two sites. For 100 published species-area relationships examined by Connor and McCoy (1979), we find that log (area) explains on average only 44.8% of the variation in log (number of species). If the forces envisioned in the equilibrium theory hypothesis are the primary determinants (or those in the random placement or disturbance hypotheses), then the residual variation in species richness should probably be viewed as either "noise" resulting from high rates of species turnover, or as

effects of island isolation. One would always choose the larger site, if it were not too isolated.

If, on the other hand, the habitat diversity hypothesis is correct, one might hypothesize that the residual variation is primarily caused by habitat differences, and there might be many times when the smaller site would be selected. It would depend on the habitats at the particular sites and the habitat requirements of particular species of conservation interest. This argument is cast in unrealistically Manichaean terms - no-one would argue that habitat should be given no consideration in refuge selection. Of course a diverse virgin forest would be preferable to a recent clearcut for almost all conservation purposes. However, the argument over relative weights to give area and habitat in conservation decisions is still a substantive one. To the extent that the equilibrium theory interpretation of the species-area relationship is correct, area *per se* should be valued. To the extent that the habitat diversity explanation is valid, area *per se* should be a secondary consideration.

East and Williams (1984) argue that autecological studies, such as those that will tell us about target species' habitat requirements, will often be unavailable, and that consideration of area alone will be a very useful substitute. In particular, for indigenous forest-dwelling birds on islands off New Zealand, they conclude that, not only is the number of species well predicted by area, but so is the composition. They detect a predictable, sequential pattern of species loss as island area decreases - each species falls out at a given area, and one can predict which species will be found on each island simply from these areas. This predictability, in turn, suggests to them that the island biotae would serve as good indicators for the sizes of refuges required on the mainland.

Here we quantify the notion of a predictable sequence of species loss with decreasing area, and apply the quantification to the New Zealand island birds as well as to passerine birds of the Cyclades Archipelago in the Aegean Sea (Watson, 1964; Simberloff, 1985). East and Williams (1984) cite Diamond (1972), Moore and Hooper (1975), Galli, Leck and Forman, (1976), and Whitcomb *et at*. (1981) as having shown a similar predictable pattern of species loss with area. Since none of these four studies lists which species are on which islands, it is impossible to assess this claim. None of the cited authors themselves make such an assertion, though Galli *et at*. (1976) observe that "new species appear

when their minimum habitat size requirements are fulfilled. We therefore conclude that the increase in bird species richness can be due to the progressive encountering of different minimum areas."

Statistical Procedures

Consider a binary matrix of species by islands, with S rows representing species and I columns representing islands. Thus a "1" in location i, j represents presence of species i on island j, while "0" represents absence. The islands are in the order smallest to largest, while the species are in the order least number of islands occupied to greatest number of islands occupied. The matrix for indigenous forest birds on 26 islands off New Zealand is depicted in Table 1, while the matrix for land birds of the Cyclades Archipelago, fortuitously also available for 26 islands, is depicted in Table 2. To say that species fall out in predictable sequence as island area decreases is to say that, in each row, no "0" will be rightward of a "1". That is, for each species there is a minimum island area such that the species is present on all those and only those islands exceeding that area. All "D's" will be in the upper left of the matrix, and all "1's" in the lower right.

How predictable is "predictable"? The hypothesis states that, for each species, there should be a line of "D's" followed by a line of "1's". Schoener and Schoener (1983) call the pattern for each species an "occurrence sequence". How much does an occurrence sequence deviate from this expectation? No deviation would consist of exactly the expected pattern, while maximum deviation would consist of the opposite pattern: a row of "1 's" followed by a row of "D's", corresponding to occupation of all the small islands and absence from all the large ones (Table 3). Any particular sequence deviates from the expectation by a given number of "transpositions". One could transform the observed sequence into the expectation by making a certain number of switches between "D's" and "1's". For example, in Table 3, the sequence depicted in row 3 could be transformed into the expected sequence by 2 transpositions, while the sequence in row 4 could be transformed to the expected sequence by 3 transpositions.

Suppose species were strewn randomly among islands, independently of the islands' areas. How unlikely would it be, under that random hypothesis, for a species to have a sequence as close to the . predicted one as the observed sequence is? Suppose that a species is found on s of 26 islands. There are $26C_s$ possible sequences: $26C_s$ sets of s islands that

Table 1: *Arrangement of birds on* 26 *islands of New Zealand. Data from East and Williams* (1984) *and East (pers. comm.* 1985) *"1" represents presence, "0" represents absence.*

											ISLANDS															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1
9	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1
S 10	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	1
P 11	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1
E 12	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1
C 13	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	1	0	1	1	1
I 14	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1
E 15	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	0	1	1	1
S 16	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
17	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	1
18	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1
19	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
20	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
21	0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1
22	0	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
23	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Species: 1-*Apteryx owenii,* 2-*Galliral/us australis,* 3-*Falco novaeseelandiae,* 4-*Callaeas cinerea,* 5-*Notiomystis cincta,* 6-*Finschia novaeseelandiae,* 7-*Eudynamys taitensis,* 8-*Mohoua albicilla* and M. *ochrocephala,* 9-*Acanthisitta chloris,* 10-*Petroica australis,* 11-*Philesturnus carunculatus,* 12-*Chalcites lucidus,* 13-*Nestor meridionalis,* 14-*Cyanoramphus auriceps,* 15-*Petroica macrocephala,* 16-*Prosthemadera novaeseelandiae,* 17-*Cyanoramphus novaezelandiae,* 18-*Hemiphaga novaeseelandiae,* I9-*Ninox novaeseelandiae,* 20-*Anthornis melanura,* 21-*Zosterops lateralis,* 22-*Gerygone igata,* 23-*Rhipidura fuliginosa.* Islands: l-Rurima, 2-Motuhoropapa, 3-Allport, 4-0pen Bay, 5-Mokohinau, 6-Motuara, 7-Alderman, 8-Whale, 9-Solander, 10-Cuvier, 11-Poor Knights, 12-Maud, 13-Chickens, 14-Chetwodes, I5-Great King, 16-Rakitu, 17-Cavalli, 18-Hen, 19-Big South Cape, 20-Major, 21-Codfish, 22-Kapiti, 23-Mercury, 24-Little Barrier, 25-D'Urville, 26-Great Barrier.

the species could have occupied. Only one of them is the predicted sequence, and each of the other arrangements requires from 1 to s x (26-s) transpositions to become the predicted sequence - the fewer the required transpositions, the more similar the arrangement is to the predicted one. Thus the position, in terms of number of required transpositions, of the observed sequence among the set of all $26C_s$ possible ones is a measure of just how predictable the sequence is.

The Appendix describes an algorithm by which one can calculate the number of different sequences requiring any given number of transpositions to be reduced to the predicted one. Thus one can calculate for each species the tail probability (that is, how many sequences require at least as many transpositions as the observed sequence).

Results

(i) *New Zealand*

These tail probabilities are depicted for the New Zealand birds in Table 4. One sees that, even though the sequences are not exactly as predicted for 21 of the 23 species, the arrangements for most species are remarkably predictable. At the 0.05 level one would have rejected the hypothesis of great predictability in favour of one of random allocation among islands for only four species, the two occupying the fewest islands, the one occupying the most islands, and the one occupying the third most islands. At the 0.10 level the hypothesis would have been rejected only for the latter two species, fantail *(Rhipidura fuliginosa)* and silvereye *(Zosterops lateralis).* Neither bird is restricted to indigenous forest and they occur widely in exotic forests as well as other highly

modified rural and urban habitats (East and Williams, 1984). Exactly why the fantail is missing from Mokohinau, and especially from Poor Knights, when it is found on smaller islands, such as Rurima, cannot be deduced from the distributional data alone, but it is these absences that are responsible for the departure from predictability. The silvereye has still more unpredictable absences, particularly from Great King and Chickens. It might require a major effort to explain the particular anomalies, and since neither bird is endemic and both can exist outside indigenous forest, it would not appear that scarce conservation resources would optimally be spent on answering these questions.

On the other hand, for little spotted kiwi *(Apteryx owenii)* and weka *(Gallirallus australis),* the two birds least widely distributed among the 26 islands, the deviation from the predicted sequence suggests that it would not be wise to attempt conservation on the mainland based solely on insular distributions. In both instances the deviation is caused by absence from the largest island, Great Barrier. East and Williams (1984) explain the kiwi's absence as a result of Great Barrier's isolation from mainland areas where the bird is present. For the weka, they note that even on the mainland its population sizes seem to fluctuate greatly, even to the point of local extinction. However, on the mainland these local extinctions can easily be redressed by reinvasion, while on islands such as Great Barrier, 19 km from the mainland, such reinvasion is much more difficult (Williams 1981). Since D'Urville is only 500 m from the mainland, it may, according to East and Williams (1984), be routinely recolonised after extinction. Because both species have been introduced to other, smaller islands of this group of 26, and have not survived even though the habitat appears favorable, East and Williams feel that they have some direct evidence that the small size of sites would suffice to preclude long-term persistence, but we see that forces other than size must be considered.

(ii) Cyclades Archipeligo
The picture for the Cyclades passerines is somewhat different (Table 5), as might be expected because the Cyclades have very little forest and thus no typical forest birds (Watson, 1964). Once again we see that the birds that occupy only one island tend to deviate from the prediction, particularly woodlark *(Lullula arborea)* and jackdaw *(Coloeus monedula),* which are both found on Kea but not on four larger islands. Watson (1964) views the distribution of

these two species as more mysterious than most of those in the Cyclades. He tentatively attributes their failure to occur on other islands to habitat deficiency, though exactly what combination of habitats is needed but absent is not clear. The jackdaw nests in rocky cliffs, but also in built-up areas; it uses cultivated land for feeding, but such land is available on all the Cyclades. The woodlark is found in many kinds of habitats outside the Cyclades. Kea is closest of these islands to the Greek mainland, so it is not inconceivable that there have been occasional invasions and extinctions, but on other islands recolonization takes a long time. Watson (1964) hypothesizes that the jackdaw may have been eliminated from some islands by density-independent forces, such as storms or disease, but there is no direct evidence.

Among birds that are much more common in the Cyclades there are also species whose occurrence sequences are far from predicted, especially white wagtail *(Motacilla alba)* and wheatear *(Oenanthe oenanthe)*. Both species are present on only a minority of islands, but the occupied islands are indistinguishable from a subset that is random with respect to size. Both these species are open country birds, and both are sufficiently common both in the Cyclades and on the mainland that one could not view them as in need of conservation measures. Nevertheless, it is certain that area alone is not a good predictor of their presence, and there is little reason to think that our predictions based on area for discrete sites on the mainland would be borne out any better. Watson (1964) feels that in the Cyclades the white wagtail is limited primarily by habitat deficiences - it is found either in damp high mountain meadows, which are scarce on the islands, or on rocky coasts. He tentatively proposes that the wheatear is excluded from some islands by competition of an unknown nature with the black-eared wheatear *(0. hispanica).*

Discussion
The species-area relationship for these two archipelagoes is quite strong. For the 26 New Zealand islands Spearman's rho is 0.878, while for the 26 Cyclades it is 0.840. This means that ca. 77.0% of the variation in ranks for species richness for the New Zealand islands can be explained by variation in ranks for area, while the analogous figure for the Cyclades is ca. 70.6%. The species-area relationship may be considered the "island's-eye view" of predictability. If larger islands always had

Table 2: *Arrangement of passerine birds on 26 islands of the Cyclades Archipelago. Data from Watson* (1964). "1" *represents presence, "0" represents absence. .*

													ISLANDS													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1
	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1
S	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1
P	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1
E	19	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1
C	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
I	21	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
E	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1
S	23	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0
	24	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1
	25	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0
	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1
	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1
	28	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1
	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1
	30	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1	1	0	1
	31	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	1	1	1	0	1
	32	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	1	1
	33	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	1	1	1	1	1
	34	0	0	0	0	1	0	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	0	1	0	0	0
	35	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	1	1	1
	36	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	1	1	1	0	0	1	1	1
	37	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	1	1	1	1
	38	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1
	39	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	1	1	1	1	0	1	1	0	1	1	1
	40	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	41	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1

Species: 1-*Lullula arborea*, 2-*Coloeus monedula*, 3- *Turdus merula*, 4-*Luscinia megarhynchos*, 5-*Erithacus rubecula*, 6-*Sylvia borin*, 7-*Motacilla cinerea*, 8-*Parus major*, 9- *Troglodytes troglodytes*, l0-*Saxicola torquata* 11-*Hippolais olivetorum*, 12-*Sylvia hortensis*, 13-*Sylvia communis*, 14-*Emberiza cirius*, 15-*Parus caeruleus*, 16-*Anthus campestris*, 17-*Motacilla flava*, 18-*Callandrella cineria*, 19-*Muscicapa striata*, 20-*Emberiza calandra*, 21-*Sylvia cantillans*, 22-*Chloris chloris*, 23-*Petronia petronia*, 24-*Ptyonoprogne rupestris*, 25-*Delichon urbica*, 26-*Hippolais pallida*, 27-*Emberiza melanocephala*, 28-*Motacilla alba*, 29-*Carduelis carduelis*, 30-*Hirundo rustica*, 31-*Lanius senator*, 32-*Emberiza caesia*, 33-*Monticola solitarus*, 34-*0enanthe oenanthe*, 35-*Sylvia melanocephala*, 36-*Acanthis cannabina*, 37-*Corvus corax*, 38-*Passer domesticus*, 39-*0enanthe hispanica*, 40-*Galerida cristata*, 41-*Corvus corone*. Islands: 1-Tourkonisi, 2-Ag Spiridon, 3-Evraiokastron, 4-Gaidaronisi, 5-Kardiotissa, 6-Tria Nisia, 7-Zephyros, 8-Makaries, 9-Ophidousa, 10-Delos, l1-Srina, 12-Antimilos, 13-Schoinousa, 14-Kouphonisia, 15-Heracleia, 16-Santorini, 17-Myconos, 18-Syros, 19-5ip nos, 20-Astypalaia, 21-Kythos, 22-Kea, 23-Milos, 24-Paros, 25-Andros, 26-Nasos.

Table 3. *Some examples of binary presence-absence matrices of species on islands. Rows are species (in order of increasing number of islands occupied) and columns are islands (in order of increasing area). Row 1 corresponds to a species that occurs in the predicted sequence. Row 2 corresponds to a species that occurs in the sequence most different from that predicted. Row 3 can be transformed to the expected sequence through 2 transpositions, while row 4 can be transformed through 3 transpositions.*

	ISLANDS				
S		1	2	3	4	5
P	1	0	0	0	1	1
E	2	1	1	0	0	0
C	3	0	0	1	1	0
I	4	0	1	1	1	0
E						
S						

Table 4. *Conformity to predictable sequence for 23 bird species on islands off New Zealand. Species as in Table 1.*

Species	Number of Islands	Number of Transpositions	Tail Probability
1	1	1	0.077
2	1	1	0.077
3	2	0	0.003
4	2	0	0.003
5	2	1	0.006
6	2	5	0.037
7	4	4	0.001
8	5	7	0.001
9	5	12	0.003
10	6	11	0.001
11	6	19	0.005
12	8	10	< 0.001
13	9	12	<0.001
14	9	20	< 0.001
15	11	30	0.003
16	13	10	< 0.001
17	13	28	0.001
18	14	23	< 0.001
19	16	17	<0.001
20	19	7	< 0.001
21	21	33	0.112
22	22	11	0.008
23	24	13	0.172

Table 5. *Conformity to predictable sequence for 41 passerine species on islands in the Cyclades Archipelago. Species as in Table 2.*

Species	Number of Islands	Number of Transpositions	Tail Probability
1	1	4	0.192
2	1	4	0.192
3	1	1	0.077
4	1	0	0.038
5	1	1	0.077
6	1	0	0.038
7	1	1	0.077
8	2	0	0.003
9	2	0	0.003
10	2	0	0.003
11	2	1	0.006
12	2	1	0.006
13	2	6	0.049
14	2	0	0.003
15	3	2	0.001
16	3	11	0.032
17	3	11	0.032
18	4	13	0.013
19	4	20	0.048
20	4	1	< 0.001
21	5	23	0.029
22	5	14	0.005
23	5	27	0.053
24	6	25	0.017
25	6	39	0.109
26	6	12	0.001
27	6	12	0.001
28	8	58	0.231
29	8	7	<0.001
30	9	18	<0.001
31	9	17	<0.001
32	10	16	<0.001
33	11	20	< 0.001
34	11	74	0.315
35	11	45	0.027
36	12	44	0.020
37	13	23	<0.001
38	13	5	< 0.001
39	14	37	0.007
40	17	5	< 0.001
41	17	41	0.029

Table 6. *Hypothetical archipelago in which ranks of species richness and island area are perfectly correlated, yet species' incidences are not all in predicted sequence. Islands, in order of increasing area, are 1, 2, 3, 4, 5.*

	ISLANDS				
S		1	2	3	4	5
P						
E	1	0	0	1	1	1
C	2	0	0	1	1	1
I	3	1	1	0	1	1
E						
S						

more species, rho would be 1.000 and all variation in ranks for species richness could be construed as variation in ranks for area. To the extent that rho is less than 1.000, we look for other reasons, like differences in habitat diversity, isolation, etc. Typically we add these as independent variables to regressions of species richness on area, though assumptions of regression analysis are violated, so that statistical significance cannot be assessed (James and McCulloch, 1985).

Looking at predictability in the way that East and Williams (1984) suggested can be considered the "species'-eye view" of predictability. If each species' occurrence sequence were exactly as predicted, with all those islands and only those islands larger than a given minimum critical area occupied by a given species, then rho for the species-area relationship would be 1.000. On the other hand, rho could be 1.000 and the species' sequences still not as predicted (Table 6). So taking the species'-eye view of deviation from predicted pattern allows us to detect anomalies that the species-area relationship would not have indicated. Furthermore, the species'-eye view causes us to focus on *which* species are responsible for deviation from expectation. Thus we are particularly drawn to explain the occupancy patterns for fantail, silvereye, little spotted kiwi, and weka. It is clear, then, that looking at the pattern as East and Williams (1984) suggested is a worthwhile exercise that may lead to new insights.

The pattern alone, however, cannot often constitute strong evidence for a particular explanation (Simberloff and Conner, 1981). Partly this is because, given the numbers of species and the numbers of islands for which data are usually available, it is difficult to show that there is a statistically significant anomaly. Even if there appears to be a statistically significant anomaly, one cannot use the same set of data to generate a hypothesis that one uses to test it (Selvin and Stuart, 1966). Yet there are no other distributional data with which to test a hypothesis about the distribution of bird species in a particular archipelago.

In some sciences experiment is used to test hypotheses, and controlled manipulation is undoubtedly the strongest sort of test. But it is difficult to see how conservation questions about these birds can be experimentally tested, at least with the island data alone. Lovejoy *et al*. (1983) have set up controlled mainland quadrats of different sizes in Amazonia and are now monitoring bird species loss

in an attempt to answer directly questions about what size refuges are necessary for what species. However, this is an expensive and extremely long-term experiment, and East and Williams (1984) as well as Diamond (1984) suggest that conservation decisions for New Zealand birds have to be made very quickly. This is the rationale for using island distributions to assess conservation suitability of mainland tracts of different sizes. Yet forest islands are not exactly like oceanic islands, and inferring processes from oceanic island distributional data is rarely convincing (Abbott, 1980). Species lists for potential forest reserves would be a sounder basis for conservation decisions than would lists for island analogs. Occurrence sequences should be analyzed for such data if sequences are to be used in conservation decisions.

Finally, it is worth reconsidering the dispute over the determinants of species-area relationships in light of the analyses of these two avifaunas. Lack (1976) argued that in virtually every instance where a bird species is absent from an island within its geographic range, the reason resides in unfulfilled habitat requirements. The particular habitat requirement may be subtle, but an insightful enough study will determine it. Watson (1964) came to exactly this conclusion about the Cyclades passerines: "When the detailed distribution of any particular species is considered, availability of suitable habitat is the paramount factor determining its pattern of occurrence. . . This point is of great significance since nearly every Aegean island is unique on the basis of its locales, size, relief, geology, soil, vegetation and human exploitation. For this reason, adjacent islands may differ strikingly and the species of birds may, therefore, likewise differ." This view is particularly interesting because the Cyclades are mostly rocky, quite barren, and superficially very similar to one another.

Watson (1964) attributed the species-area relationship for the Cyclades passerines to explanation (b), area as a surrogate for habitat diversity. He doubted that there was much short-term turnover, as explanation (c) demands. There is no particular reason to think that the determinants of bird species diversity, and of presence and absence of particular species, need be the same in each archipelago, however. Diamond (1984) agrees that habitat considerations plus human disturbance in the New Zealand islands are major determinants of bird distributions, but believes there is a considerable residue of absences left unexplained by these causes,

and that there is no better reason for these than continuing "normal" turnover. Perhaps he is correct and, even if he is not, he and East and Williams (1984) contend that it would take too long (for conservation purposes) to determine the specific habitat requirements of the various species.

It would nevertheless be informative to have actual demonstration of turnover on the small islands, and in the small mainland patches. It is also possible that simply focusing on area could lead to suboptimal conservation choices, and one could make valuable guesses about habitat types and diversity without actually doing all the autecological research. For example, Kitchener et al. (1980) show that scattered small reserves contain almost all the lizards of the Australian wheatbelt, so long as the reserves have the right habitats. If all available forests can be saved, then they should be and there is no need for further analysis. If, on the other hand, choices have to be made and some patches sacrificed, it is possible that the optimal selection will not rest only or even primarily on area.

The main argument against such a course, and in favour of always taking larger reserves, is the probability of higher of species loss from smaller sites (e.g., Soule, Wilcox and Holtby, 1979). However, the species loss has very rarely been observed, only inferred, and the statistical methods have been so weak that one often cannot preclude the possibility that there is virtually no species loss for millennia unless sites are extremely small (Boecklen and Gotelli, 1984). It seems peculiar to place so much credence in an inferred process. It is seductive to think that as easily measured a variable as area can be a satisfactory conservation criterion, but easy courses are often not best in the long run.

We are reminded of Raleigh's poem, "The nymph's reply to the shepherd," in which the girl responds skeptically to the passionate shepherd's glib promises of quick pleasures, "If all the world and love were young, And truth in every shepherd's tongue". With this beginning, she questions the long term value of his offerings. Conservation biologists are similarly presented with easy answers, but a seduction may turn out to be costly.

Acknowledgements

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Appendix

Consider k cells, occupied by m l's and k-m 0's. The position numbers of the cells, from right to left, are 1,2, . . ., k-l, k. Let $a_i = 1$ if the ith cell is occupied by a "1", and $a_i = 0$ if the ith cell is occupied by a "0". Let D, the "transposition distance", be defined as the number of transpositions of adjacent cells required so that the m 1's are in the rightmost positions, 1 through m. Then it is easily shown that:

$$(1)\quad D = \sum_{i=1}^{k} a_i - m(m+1)/2$$

For any given pair of integers (k,m), any arrangement with the same Σa_i therefore gives rise to the same transposition distance, D. The problem then reduces to finding how many ways (W) a given integer $M = \Sigma a_i = D + m(m+1)12$ can be expressed as the sum of m distinct positive integers, each $\leq k$.

It is easy to show that if we define

$$(2)\quad f_k(x,y) = (1+xy)(1+xy^2)(1+xy^3) \ldots (1+xy^k)$$

then W = coefficient of $x^m y^M$ in $f_k(x,y)$. Now define a bivariate random variable (U_n,V_n) such that:

$$(3)\quad (U_n,V_n) = (0,0) \text{ with probability } 1/2$$
$$(U_n,V_n) = (l,n) \text{ with probability } 1/2$$

The probability generating function for (U_n,V_n) is:

$$(4)\quad \phi_{(U_n,V_n)}(x,y) = E(x^{U_n}y^{V_n}) =$$

$$\sum_{U_n,V_n} x^{u_n}y^{v_n}\Pr(U_n = u_n, V_n = v_n)$$

$$= x^o y^o \cdot 1/2 + x^1 y^n \cdot 1/2 = 1/2 \cdot (1+xy^n)$$

Consider k independent random variables $(U_1,V_1,)$, . . .,(U_k,V_k), where each is of the form (U_n,V_n) above, and define a new random variable:

$$(5)\quad (U^*,V^*) = \sum_{i=1}^{k} (V_i,V_i)$$

Then the probability generating function for (U^*, V^*) is:

$$(6)\quad \emptyset(U^*,V^*)^{(x,y)} = \emptyset_{(\sum_{i=1}^{k}(U_i,V_i))}(x,y)$$

$$= \prod_{i=1}^{k} \emptyset(U_i,V_i)^{(x,y)}$$

$$= (1/2)^k \prod_{i=1}^{k} (1+ xy^i) = (1/2)^k f_k(x,y)$$

Therefore $f_k(x,y) = 2^k \emptyset(U^*,V^*)^{(x,y)}$, and this latter expression, by the definition of probability generating function (Feller, 1968), equals $2^k \sum_{u^*,v^*} x^{u^*}y^{v^*} \Pr(U^* = u^*,V^* = v^*)$.

Since W = the coefficient of $x^m y^M$ in $f_k(x,y)$,

$$(7)\quad W = 2^k \Pr(U^* = m,V^* = M)$$

$$= 2^k \Pr(\sum_{i=1}^{k} U_i = m, \sum_{i=1}^{k} V_i = M)$$

But $V_i = iU_i$, so

$$(8)\quad W = 2^k \Pr(\sum_{i=1}^{k} U_i = m, \sum_{i=1}^{k} iU_i = M)$$

$$= 2^k \Pr(\sum_{i=1}^{k} U_i = m)\Pr(\sum_{i=1}^{k} iU_i = M| \sum_{i=1}^{k} U_i = m) = 2^k \cdot A \cdot B$$

Now we need expressions for A and B.

$$(9)\quad A = \Pr(\sum_{i=1}^{k} U_i = m) = \Pr(m \text{ of the } U_i\text{'s} = 1$$

and the remaining k-m of the U_i's = 0)

Since the U_i are independent 0,1 random variables, with probabilities 1/2 of taking the value 0 and 1/2 of taking the value 1,

$$(10)\quad \Pr(\sum_{i=1}^{k} U_i = m = \Pr(m \text{ success in k independent Bernouilli trials, each with p = 1/2})$$

$$= \binom{k}{m}(1/2)^k$$

$$(11)\quad 2^k A = \binom{k}{m}$$

For B, we must find $\Pr(1U_1 + 2U_2 + ... + kU_k) = M$ given that $\sum_{i=1}^{k} U_i = m$.

We can view (1,2 . . .,k) as k ranks, and $(1U_1 + 2U_2 + ... + kU_k)$ as the sum of the ranks associated with the subset of U_i'S (U^1) for which $U_i = 1$. In other words we want the sum of the ranks of elements of U^1 given that the number of elements in U^1 is m.

But this is the Wilcoxon 2-sample rank-sum statistic, R, for 2 samples of sizes m and k-m, respectively. Thus B = Pr(R = M | k,m), and

$$(12)\quad w = w_m^k(M) = \binom{k}{m} \Pr(R = M|k,m)$$